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THE MALE WARNING VIBRATION IN *BUFO*¹

BY ALBERT P. BLAIR²

When sexually excited, male toads of the genus *Bufo* attempt amplexus with virtually any moving object of approximately their own size. Practically, this usually means a male or female toad. Aronson (1944) has shown that in the laboratory male *Bufo americanus* clasp male toads quite as readily as they do females. However, for the conservation of the reproductive potential of the species, it is imperative that some mechanism insure quick release of clasped males. This mechanism has been shown (Aronson, 1944) to be in the nature of a warning vibration given by males when clasped by other males. The warning vibration is given when the male is touched on the back, sides, and sometimes on the top of the head and the hind legs; contact on the throat or ventral side of the toad does not elicit the warning vibration. The method of production of this vibration is not known. It is probably under hormonal control, since it can be elicited in juvenile males by treatment with amphibian and mammalian gonadotrophins and in juvenile toads of either sex by treatment with testosterone propionate (Blair, 1946). The material presented here is in the nature of a comparative study of the male warning vibration in seven species of toads.

Male toads available were as follows:

NO.	SPECIES	SOURCE
9	<i>B. terrestris</i>	Silver Springs, Fla.
7	<i>B. fowleri</i>	Upton, N. J.
6	<i>B. woodhousii</i>	Dallas, Texas
2	<i>B. alvarius</i>	Tucson, Arizona
20	<i>B. marinus</i>	Monterrey, N. L., Mexico
50	<i>B. valliceps</i>	Monterrey, N. L., Mexico
2	<i>B. cognatus</i>	Tucson, Arizona

These animals had been in the laboratory, during which time they had been fed on mealworms, cockroaches, and blowflies, for one to four months. All males exhibited the warning vibration when handled. To induce clasping reflex and possibly to heighten the warning vibration, males were injected with fresh whole anterior pituitary of female *Rana pipiens*. Pituitary treatment failed to induce clasping reaction in *B. cognatus* and *B. marinus*.

For comparison of vibrations, kymograph records were made (figs. 1 and 2). A metronome was used to give a one-half second time signal. To the kymograph lever was attached, by means of a movable joint, a rigid metal arm which terminated in a flexible U-shaped clamp. In making a recording, the clamp was placed over the body of the toad with the tips of the arms of the clamp in contact with the sides of the toad. The clamp then served both to stimulate the warning vibration and to transmit the vibration to the lever tracing the record on the smoked drum.

Table 1 summarizes the data on counts of vibrations per second of the toads under consideration. It is apparent that the toads may be divided into three general classes with respect to the number of warning vibrations per second: (1) those with a high frequency (*B. woodhousii* and *B. fowleri*), (2) those with an intermediate frequency (*B. terrestris*), and (3) those with a low frequency (*B. cognatus*, *B. valliceps*, *B. marinus*, and *B. alvarius*). *Bufo woodhousii* and *B. fowleri* are morphologically very similar and have been considered by many workers to be subspecifically related. *Bufo terrestris* is a member of a species complex which includes *B. americanus*, *B. fowleri*, and *B. woodhousii*; its closest rela-

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²Department of Animal Behavior.

TABLE 1
WARNING VIBRATIONS PER SECOND

Species	Number of Individuals	Total Number of Tests	Number of Vibrations Mean	Number of Vibrations per Second Range
<i>B. cognatus</i>	2	7	6.5	5-9.5
<i>B. valliceps</i>	12	40	13.0	9.5-16
<i>B. marinus</i>	3	15	6.9	5-9
<i>B. alvarius</i>	1	4	5.0	5
<i>B. woodhousii</i>	5	12	93.2	84-104
<i>B. fowleri</i>	3	11	93.3	80-104
<i>B. terrestris</i>	9	30	51.3	42-64

tive is *B. americanus*, this relationship having been denoted as subspecific by some recent investigators (Burt, 1938; Netting and Goin, 1946). The four toads with low number of warning vibrations do not constitute a natural group. However, *B. valliceps*, *B. marinus*, and *B. alvarius* are probably more closely related to one another than they are to the *americanus-terrestris-fowleri-woodhousii* complex or to *B. cognatus*. *Bufo cognatus* is a member of a complex which includes *B. compactilis*; although no counts are available, gross observations indicate that *B. compactilis* has the slow vibration found in *B. cognatus*. To a considerable extent, then, vibration frequency may be considered indicative of taxonomic relationship.

The question arises as to the efficacy of slow vibrations in causing release of a male toad with rapid vibrations, and vice versa. Where slow- and rapid-vibrating species occur in the same breeding ponds (*B.*

valliceps and *B. fowleri* in Texas and Louisiana, *B. woodhousii* and *B. cognatus* in the Great Plains) any failure to respond to vibrations of lesser or greater frequency would seem to constitute a barrier to efficient reproduction.

To answer this question extra-specific clasping experiments were conducted. Since there is a fatigue factor in the clasping reaction, males were occasionally allowed to clasp females to determine that the clasping reaction was still present. In general, male toads will not clasp toads much smaller than they are. The seven species of toads used in these experiments may be grouped in two size classes, large (*B. marinus* and *B. alvarius*), and medium (*B. valliceps*, *B. cognatus*, *B. woodhousii*, *B. fowleri*, and *B. terrestris*). No experiment was attempted in which a male toad of the "large" class clasped male or female toads of the "medium" class.

1. EXPERIMENTS WITH ♂ *B. FOWLERI*

B. fowleri No. 1

Placed on	Released spontaneously after	Forcibly removed after
♀ <i>fowleri</i>	12", 7"	5'
♂ <i>fowleri</i>		5'
♂ <i>valliceps</i>	59", 4½"	
♂ <i>woodhousii</i>	3", 4"	
♂ <i>fowleri</i>	8", 3"	
♂ <i>cognatus</i>		5'
♀ <i>fowleri</i>	8", 4"	
♂ <i>terrestris</i>	12", 2", 4"	
♂ <i>woodhousii</i>		
♀ <i>fowleri</i>	1½', 1'	5'
♂ <i>valliceps</i>		10'
♀ <i>terrestris</i>		
♂ <i>cognatus</i>	18", 9"	
♂ <i>valliceps</i>	6", 2"	
♀ <i>fowleri</i>		10'
♀ <i>valliceps</i>		20'
♀ <i>terrestris</i>		5'

B. fowleri No. 2

¹ *B. valliceps* definitely vibrating.

$\text{\female } fowleri$		5'
$\text{\male } cognatus$	22", 4"	
$\text{\male } valliceps$		10'
$\text{\male } fowleri$	7", 1"	
$\text{\male } terrestris$	2", 2"	
$\text{\male } woodhousii}$	7", 3"	

2. EXPERIMENTS WITH $\text{\male } B. WOODHOUSII$

$B. woodhousii$ No. 1	Placed on	Released spontaneously after	Forcibly removed after
	$\text{\female } terrestris$		8'
	$\text{\male } cognatus$	35", 3"	
	$\text{\female } terrestris$		5'
	$\text{\male } woodhousii}$	7", 3"	
	$\text{\male } marinus}$		8'²
	$\text{\male } alvarius}$		10'²
	$\text{\male } valliceps$	15", 3"	
	$\text{\male } fowleri}$	3", 2"	
	$\text{\male } marinus}$	8", 15"	
	$\text{\female } terrestris}$		10'

3. EXPERIMENTS WITH $\text{\male } B. TERRESTRIS$

$B. terrestris$ No. 1	Placed on	Released spontaneously after	Forcibly removed after
	$\text{\female } terrestris}$		5'
	$\text{\male } valliceps$	2³/₄", 45"²	
	$\text{\male } fowleri}$		5'
	$\text{\male } cognatus}$	22", 3"	
	$\text{\female } valliceps}$		5'
	$\text{\male } woodhousii}$	4", 3"	
	$\text{\female } fowleri}$		5'
	$\text{\male } terrestris}$	2", 1"	
	$\text{\male } valliceps}$	2", 3"	
	$\text{\female } terrestris}$		5'
	$\text{\male } woodhousii}$	2", 1"	
	$\text{\male } cognatus}$	1", 1"	
	$\text{\female } valliceps}$	4', 1'	
	$\text{\female } terrestris}$		10'
	$\text{\female } valliceps}$		20'
	$\text{\male } marinus}$		6'³
	$\text{\male } terrestris}$	5", 4"	
	$\text{\male } valliceps}$	15", 4"	
	$\text{\female } terrestris}$		15'
	$\text{\male } terrestris}$		5'
	$\text{\male } valliceps}$	1¹/₄", 2"	
	$\text{\female } valliceps}$	1', 1'	
	$\text{\female } terrestris}$		10'
	$\text{\male } woodhousii}$	20", 5", 2"	
	$\text{\male } cognatus}$	4", 3"	
	$\text{\female } terrestris}$		7'
	$\text{\male } terrestris}$	1", 2"	
	$\text{\male } valliceps}$	2", 2"	
	$\text{\female } fowleri}$	1', 30"⁴	
	$\text{\female } terrestris}$		5'⁴
	$\text{\female } fowleri}$	1', 20"⁴	
	$\text{\female } terrestris}$		10'⁴

¹ $B. valliceps$ definitely vibrating.

² Toad clasped definitely vibrated.

³ $B. marinus$ vibrating vigorously.

⁴ These records are suggestive of sexual isolation; however, it is not the intent of this investigation to inquire into the question of sexual isolation in toads.

<i>B. terrestris</i> No. 3	♀ <i>fowleri</i>	20'
	♂ <i>S. couchii</i> ¹	1 ^{1/3} '
	♀ <i>fowleri</i>	10'
	♂ <i>terrestris</i>	1', 5"
	♀ <i>fowleri</i>	5'
<i>B. terrestris</i> No. 4	♀ <i>terrestris</i>	10'
	♂ <i>terrestris</i>	4", 5"
	♀ <i>terrestris</i>	10'
	♂ <i>S. couchii</i>	33", 8"
	♀ <i>terrestris</i>	5'
	♂ <i>valliceps</i>	25", 10 ^{1/2}
	♀ <i>terrestris</i>	5'
	♂ <i>marinus</i>	12 ^{1/2}
	♂ <i>cognatus</i>	25", 3"
	♂ <i>marinus</i>	5 ^{1/2}
	♀ <i>terrestris</i>	5'
	♂ <i>terrestris</i>	4", 2"

4. EXPERIMENTS WITH ♂ *B. ALVARIUS*

<i>B. alvarius</i> No. 1	Placed on	Released spontaneously after	Forcibly removed after
	♀ <i>alvarius</i>		6'
	♂ <i>alvarius</i>	5 ^{1/3}	
	♀ <i>alvarius</i>		8'
	♂ <i>marinus</i>	2'	
<i>B. alvarius</i> No. 2	♂ <i>alvarius</i>		12 ^{1/4}
	♂ <i>marinus</i>	3", 2"	
	♀ <i>alvarius</i>		10'
	♂ <i>alvarius</i>	8 ^{1/5}	
	♂ <i>alvarius</i>	2 ⁶	
	♂ <i>marinus</i>	2"	

5. EXPERIMENTS WITH ♂ *B. VALLICEPS*

<i>B. valliceps</i> No. 1	Placed on	Released spontaneously after	Forcibly removed after
	♂ <i>woodhousii</i>	6", 4"	
	♀ <i>valliceps</i>		8'
	♂ <i>valliceps</i>	1 ^{1/4} ', 6"	
	♀ <i>valliceps</i>		6'
<i>B. valliceps</i> No. 2	♂ <i>cognatus</i>	6", 4"	
	♀ <i>valliceps</i>		10'
	♂ <i>woodhousii</i>		10 ^{1/2}
	♂ <i>valliceps</i>	13", 16"	
	♂ <i>marinus</i>	2'	
	♀ <i>valliceps</i>		30'
	♂ <i>cognatus</i>	1 ^{1/2} "	
	♀ <i>valliceps</i>		10'
	♂ <i>terrestris</i>	23"	
	♀ <i>valliceps</i>		15'
	♂ <i>woodhousii</i>		15 ^{1/2}
	♂ <i>cognatus</i>	12"	
	♂ <i>terrestris</i>	5"	
	♀ <i>valliceps</i>		30'

¹ *Scaphiopus couchii* belongs to a different family, Pelobatidae. When seized, the male utters a croak accompanied by a vibratory body movement. The animals used were from Tucson, Arizona.

² Clasped ♂ vibrated vigorously.

³ Clasped ♂ had rather weak vibration.

⁴ Clasped ♂ did not vibrate.

⁵ Clasping ♂ released on third vibration.

⁶ Clasping ♂ released immediately on first vibration.

⁷ Clasped ♂ chirped and vibrated vigorously.

6. EXPERIMENTS WITH ♂ S. COUCHII

S. couchii No. 1	Placed on	Released spontaneously after	Forcibly removed after
	♀ <i>terrestris</i>		5'
	♂ <i>valliceps</i>	2", 3"	3'
	♀ <i>terrestris</i>		
	♂ <i>terrestris</i>	5", 3"	3'
	♀ <i>terrestris</i>		

While results are not completely clear cut, certain tentative conclusions may be drawn. Of the *fowleri*-*woodhousii*-*terrestris* group, the vibration of any one is usually sufficient to effect release by a male of any species of the group. In two observations on a single individual, the rapid vibration of *B. woodhousii* was found effective in securing release from *B. valliceps*, which has a slow vibration. But in two observations on another individual, the rapid vibrations of *B. woodhousii* were ineffective in causing release from *B. valliceps*, though the rapid vibrations of *B. terrestris* were effective. The slow vibrations of *B. valliceps*, *B. alvarius*, and *B. marinus* are not so effective as rapid vibrations in securing release from the clasp of males of the rapid-vibrating group. The slow vibrations of *B. marinus* are effective in securing release from *B. alvarius*, which has a slow vibration. The

slow vibrations of *B. cognatus* are very effective in securing release from both rapid- and slow-vibrating toads. Why the slow vibrations of *B. cognatus* should be so much more effective than those of *B. valliceps* in securing release from the clasp of rapid-vibrating toads is not at this time apparent.

In general, it would seem that failure of male toads to respond to vibration frequencies of other than their own species constitutes no serious problem in reproduction, with the possible exception of *fowleri*-*valliceps* pairs. The extent of such difficulty can be determined only by intensive field observations.

It is of interest that *Scaphiopus couchii*, a member of a different anuran family, readily releases male *Bufo* when the clasped toad vibrates. Furthermore, male *Bufo* will not maintain a clasp on male *S. couchii*.

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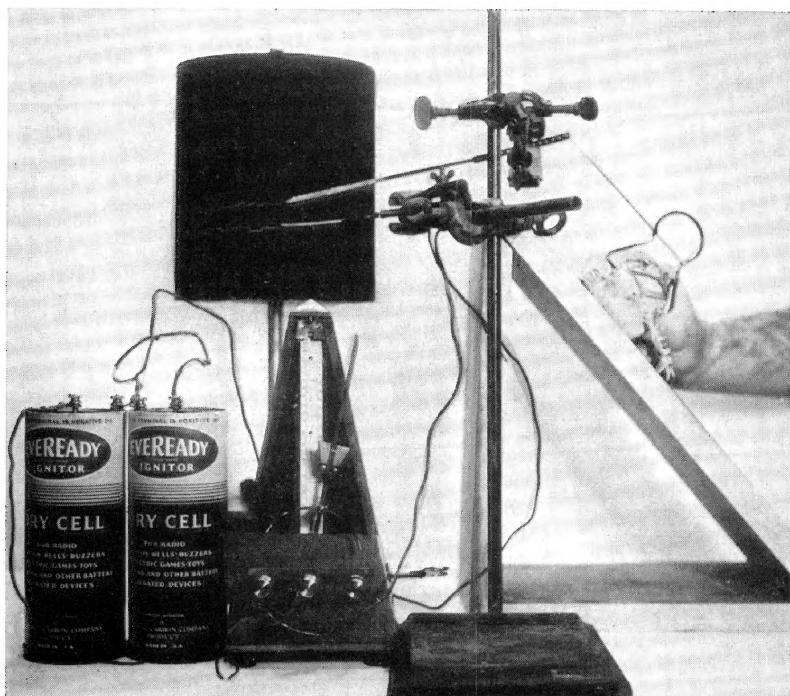


Fig. 1. Apparatus for recording vibrations.

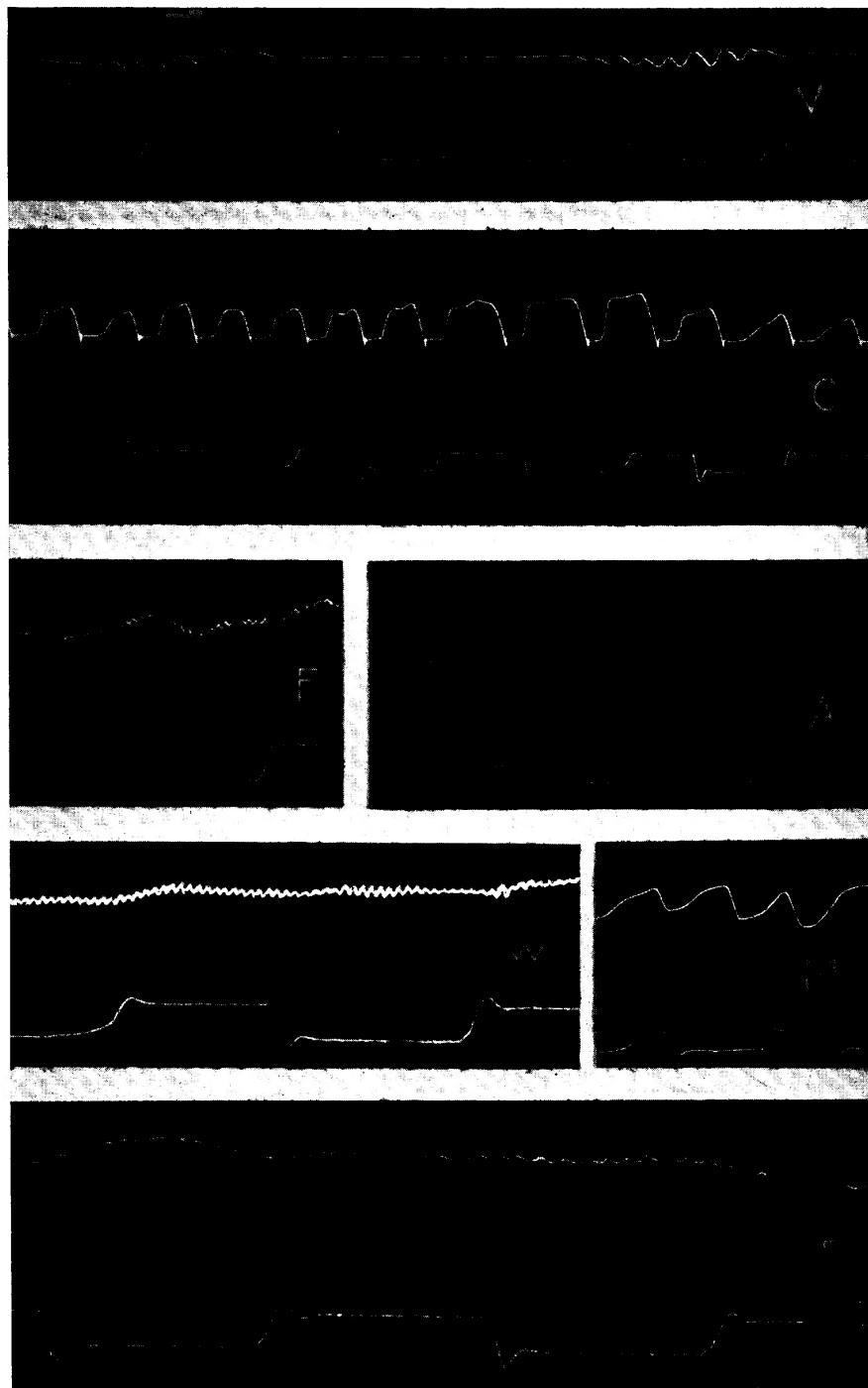


Fig. 2. Kymograph records of vibrations: V, *valliceps*; C, *cognatus*; F, *fowleri*; A, *alvarius*; W, *woodhousii*; M, *marinus*; T, *terrestris*.

